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Small-scale patterns in community structure of *Sarracenia purpurea* inquilines

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Abstract: We examined the environmental factors associated with community structure in the inquiline communities of the purple pitcher plant (*Sarracenia purpurea* L.). We sampled all 141 communities in a 10- x 20-m grid and recorded their spatial relationships to determine the relative influence of environmental and spatial factors on community structure. Environmental and spatial factors contributed equally to the variance in community composition (species identity and abundance) among pitchers. The species richness of communities was influenced by both spatial and environmental variables, particularly environmental variables related to community size. In addition, our study suggests a number of hypotheses about factors influencing community structure (e.g. predation) that could be tested experimentally.

Abbreviations: ANOVA – Analysis of Variance, DCCA – Detrended Canonical Correspondence Analysis.

Nomenclature: Patterson (1996) for protozoans.

Introduction

Each species in a community may interact with and respond to the environment at a different spatial scale. Therefore, the spatial scale at which we quantify entire communities will influence our understanding of community patterns, and an important first step in understanding any system should be to identify the spatial scales at which different patterns emerge (Dale 1999). The scale of sampling is especially important in a patchy environment, where patch size and number may influence the relative importance of species interactions and dispersal properties (Leibold and Miller 2004). Analysis of species composition and abundance data in a spatial context reveals a more complete picture of community structure and can be used to develop hypotheses about causal mechanisms (Tilman and Kareiva 1997).

Examination of the structure of a given community requires sampling and analysis of variation in the individual abundance of each species in a spatial context. Species' distributions and their relationships to environmental variables at different scales have been determined and analyzed for a range of taxa and guilds in many different systems (e.g., by Tilman and Kareiva 1997, Dale 1999). Studying an *entire* community in this way is more difficult, however, and has seldom been attempted. At least three important factors contribute to this difficulty: (1) most communities cannot be easily measured at naturally defined, discrete scales; (2) quantifying every species in a community can be difficult when many species in a range of taxa are considered; (3) a range of spatial scales must be considered, requiring considerable sampling effort.

The community structure of the inquiline communities in the water-filled pitchers of the purple pitcher plant (*Sarracenia purpurea* L.) has not been studied in a spatially explicit context within a local area, although patterns in species richness have been examined at a continental scale (Buckley et al. 2003). This system is ideal for study of community structure in a spatial context because each *S. purpurea* population consists of patchily distributed plants within a discrete bog or savannah, and each plant has a rosette of pitchers, each of which forms a spatially discrete container for an inquiline community. These communities can therefore be sampled at two natural, discrete scales within a given population of *S. purpurea*: the among-plant scale (hereafter 'plant scale') and the among-pitcher scale ('pitcher scale'). Our study was intended to examine patterns in inquiline community structure within a single population of *S. purpurea*. We analyzed species patterns in a spatial context to measure and account for spatial autocorrelation among communities at this local scale.

Because of the short time scale over which interactions occur and the discrete spatial structure of the pitchers, pitcher-plant inquiline communities are both a model system for addressing general questions about spatial pattern and community ecology (see, e.g., Bradshaw et al. 2000, Armbruster et al. 2001, Miller et al. 2002b, Miller and Kneitel in press) and communities that receive attention in their own right (see, e.g., Addicott 1974, Harvey and Miller 1996, Ellison and Gotelli 2001).

We studied the structure and community composition of pitcher inquiline communities in a spatially explicit context to address the following questions: (1) How much variation in species composition of these inquiline communities occurs at the pitcher and plant scales, and can it be predicted by environmental and spatial variables at either scale? (2) What are the important environmental predictors of variation in pitcher-inquiline-community species richness, and at what scale(s) are they important? (3) Can the presence or absence of individual species be predicted by environmental variables?

Materials and methods

Natural history of the community

The inquiline communities found within individual pitchers of *S. purpurea* have been described in several previous studies (Addicott 1974, Miller et al. 1994, Miller and Kneitel in press). Pitchers passively capture and drown prey (insects, primarily ants), which form the detritus that is the primary nutrient input in the community. Bacteria feed on detritus and make up the resource base for higher trophic levels in the community (Cochran-Stafira and von Ende 1998). Higher trophic levels include protozoa and the bdelloid rotifer *Habrotrocha rosa* (Bateman 1987, Blèdzki and Ellison 1998), the histiostomatid mite *Sarraceniopus gibsoni* (an obligate inquiline; Fashing and O'Connor 1984), and occasional copepods and cladocerans. Communities usually include the larvae of two obligately inquiline dipterans, the mosquito *Wyeomyia smithii* and the chironomid *Metriocnemus knabi* (a third known specialist, *Fletcherimyia fletcheri*, is not common in north Florida; Harvey and Miller 1996). Mosquito larvae primarily filter-feed on rotifers and protozoans (Kneitel and Miller 2002), whereas chironomid larvae feed directly on drowned prey captured by the pitcher (Heard 1994a). The plant absorbs the nutrients that are released into the pitcher fluid by this inquiline community (Blèdzki and Ellison 1998).

Species interactions within a pitcher have been investigated in several previous studies (e.g., Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002, Miller et al. 2002a), but larger-scale community patterns, such as the determinants of the occurrences of individual taxa in particular pitchers and the mechanisms that generate them, are poorly understood (Harvey and Miller 1996). At the scale of a single pitcher, both predation and resource availability can influence inquiline community composition (Kneitel and Miller 2002). At larger scales, we might expect environmental variables such as soil moisture or climate to influence the shape, size, and distribution of pitcher plants, although this influence has not been examined previously. The physical structure of the pitchers may then, in turn, affect the composition of the inquiline community, e.g., by influencing mosquito egg deposition, dispersal probability among communities, prey capture rate, or community size (Cresswell 1993, 1998, Heard 1994b). Also, the bacterial and protozoan community compositions of pitchers on the same plant are likely to be more similar than those of pitchers on different plants, if dispersal is largely local (Harvey and Miller 1996). Previous work has demonstrated that some protozoan species are dispersal limited and others are not (Miller et al. 2002b) and that increased dispersal among suites of pitcher also increases the diversity in the bacteriovore component of the community (Kneitel and Miller 2003). The dispersal mechanisms are largely unknown in this system but may include splashing from nearby pitchers during rainstorms, droplets of water carried on insects or other organisms that move from pitcher to pitcher, and cysts that float in the wind (Maguire 1963, Revill et al. 1967, Schlichting and Sides 1969).

Field sampling

Our study was conducted at the Crystal Savanna, Apalachicola National Forest, in Liberty Co., Florida, USA. This area has moist, sandy soils, a mean annual rainfall of 165 cm, and a mean annual temperature of approximately 20°C. The savanna is located along the edge of a longleaf pine (*Pinus palustris*) forest stand, bounded on one side by a thicket of titi (*Cyrilla racemiflora*) bordering a small creek. The site has a natural moisture gradient; soil moisture declines with increasing distance from the creek edge. The savanna is dominated by wire grass (*Aristida stricta*); it also harbors the purple pitcher plant (*Sarracenia purpurea*) and a variety of other carnivorous plants, including *S. flava*, *S. psitticina*, *Pinguicula lutea, P. planifolia*, and *Utricularia* sp.

On 24 March 2001, we exhaustively sampled all pitcher communities of *Sarracenia purpurea* within a 10 x 20-m grid, where the long axis followed the natural moisture gradient at the site. The grid site was chosen for its location along the moisture gradient and its moderate density of pitcher plants. The location of each plant was recorded as *x,y* coordinates to the nearest 5 cm. The grid encompassed 26 plants (0.13 plants/m^2). Of the 188 pitchers on these plants, 141 (75%) contained more than 0.5 ml of water. The fluid from each of those 141 pitchers was removed and placed in a separate sterile 50-ml centrifuge tube with a sterile, plastic pipette. We failed to collect data on certain taxa for 12 of the pitchers: these were excluded from the analyses.

We measured environmental variables to assess their relationship to community structure. The volume of fluid (ml), height of the aperture lip above the leaf base (cm), and aperture diameter (cm) were measured for each pitcher. Gravimetric soil moisture and percent organic matter were determined from a 15-cm-deep soil core taken near the base of each plant.

Species identification and enumeration

The abundances of the three major groups of organisms found in the pitcher fluid – invertebrates (including rotifers), protozoa, and bacteria – were determined. We counted individual mosquito larvae, chironomid larvae, copepods, cladocerans, and mites in the entire sample from each pitcher under a dissecting microscope. We counted protozoans and rotifers in a standard subsample (0.1 ml) using a Palmer counting cell and calculated concentration per milliliter for each species (Patterson 1996). Where possible, we identified the protozoans, according to Patterson (1996). We probably underestimated the diversity by lumping together several species within a genus (e.g., *Bodo* sp.), but these groups appeared to be dominated by single types, so the presence of rare types should not influence the results. We censused the bacteria from 10^{-3} and 10^{-5} serial dilutions and counted colonies on full-strength Plate Count Agar agar (Naomi Ward, personal communication). After three days' growth, colonies of each type were counted. Bacteria were identified solely as morphotypes: identifying the individual species was beyond the scope of our study.

Data analysis

We standardized abundance of each species by expressing it as a percentage of the maximum abundance of that species (Quinn and Keough 2002). This standardization was necessary because the taxa were sampled in different ways and raw abundances therefore differed by many orders of magnitude. Mean percent similarity (Scheiner 1992) was calculated at the pitcher and plant scales from standardized species abundances so that variation in species composition could be compared.

At both the pitcher and plant scales, following Borcard et al. (1992), partial detrended canonical correspondence analysis (DCCA) was used to relate the environmental matrix and the spatial matrix to the variance in the species abundance matrices (CANOCO for Windows Ver. 4.5; ter Braak and Smilauer 2002). This method allowed us to partition the variance in the species data into purely environmental, purely spatial, spatially structured environmental, and undetermined components (Legendre and Legendre 1998). Detrending was necessary because the gradient lengths calculated from just the species abundance data by detrended correspondence analysis at both scales were greater than four standard deviations (ter Braak 1995). Initial analyses that included the entire set of species data showed that the ordinations at both the pitcher and plant scales were driven by rare species. Consequently, reduced sets of data, which only included species that occurred in at least 10% of pitchers, were used at both plant and pitcher scales (the CANOCO downweighting option produced similar results). We could therefore examine gradient variation in the community, which was obscured by abundance outliers in the analysis of the full data. To determine whether functional groups contributed differently to the analyses, we divided the species scores from the DCCA into three groups: bacteria, bacteriovores (protozoa, rotifers, and mites), and larger invertebrates (primarily dipterans). One-way ANOVAs with functional group as a fixed effect were used to determine whether the groups differed in DCCA species scores.

The environmental variables included in the ordinations were number of pitchers per plant, pitcher fluid volume, pitcher aperture diameter, amount of moisture in the surrounding soil, and amount of organic material in the surrounding soil. Inflation factors associated with each environmental variable in analyses at both plant and pitcher scales showed that colinearity in the environmental data did not confound interpretation of the results, and all measured variables could be included. Inclusion of the categorical variable ‘plant’ (i.e., the rosette of pitchers on a given plant) at the pitcher scale did not increase the amount of species variation explained, so this variable was not included in the analysis.

A spatial matrix using the coordinates for each plant was used to examine spatial patterns in the species data. This matrix consisted of all terms for a cubic trend surface regression, i.e., $x, y, x^2, y^2, xy, x^2y, xy^2, x^3$, and y^3. This method ensured that not only linear patterns in the richness data could be extracted but also more complex spatial patterns like patches and gaps. The inclusion of the spatial data allowed us to quantify the degree to which species composition was affected by spatial autocorrelation among plants and among pitchers on plants, and it allowed us to remove this effect from the analysis, so that the importance of other environmental gradients could be considered.

To determine the best predictors of species richness at the pitcher scale, we used backwards, stepwise generalized linear mixed models with Poisson error distribution and the categorical variable ‘plant’ as a random effect (SAS version 8.0, macro GLIMMIX; SAS Institute 1999-2000). We could therefore determine the important predictors of pitcher richness while preventing pseudoreplication in the analysis (a problem because pitchers on the same plant are not independent).

To determine the best predictors of species richness at the plant scale, we also used backwards, stepwise generalized linear mixed models with Poisson error distribution (SAS version 8.0, procedure GENMOD; SAS Institute 1999–2000) to regress richness on the spatial and environmental variables. Means of environmental variables measured at the pitcher scale were used as predictors in the analysis at this scale.

We used backwards, stepwise logistic regression (SAS version 8.0, macro GLIMMIX; SAS Institute 1999-2000) to determine the best predictors of the presence of the seven species that occurred in more than 20% of pitchers. Again, we used the categorical variable ‘plant’ as a random effect to prevent pseudoreplication at the pitcher scale. In addition, the species richness of the three main classes of organisms (invertebrates, protozoans, and bacteria) were included as predictors in an attempt to investigate potential interactions among the inquilines; for each species only the two classes in which that species did not occur were included as predictors.

Results

In the fluid collected from pitchers, 8 invertebrate species, 22 protozoan species, and 20 bacterial colony types were encountered. Pitchers contained between 0 and 15 species (mean = 6), and plants contained between 1 and 30 (mean =14).

Variation among pitchers in species composition

The mean percent compositional similarity for pitchers was 15%, meaning that, on average, any two pitchers examined shared only 15% of their species. At the plant scale the mean percent similarity was slightly higher, 24%.

The first two axes of the DCCA explained 18.4% of the variation in species composition among pitchers. Environmental and spatial data explained 22% of the total variation. The partial DCCA showed that approximately equal amounts of the variation in community composition were explained by environmental factors (9%) and spatial factors (10%), and only 3% was identified as spatially structured environmental variation, so environmental variables were not strongly spatially autocorrelated within the plot.

After spatial structure in the data was taken into account by use of data in the spatial matrix as covariables in the analysis, the DCCA revealed two gradients in species composition, represented by the Axis 1 and Axis 2 DCCA site scores (Fig. 1A), which were both statistically significant ($P < 0.05$) and correlated with environmental variables. Axis 1 represents a gradient in soil moisture and organic matter, as well as pitcher size and fluid volume. Axis 2 represents a gradient in pitchers per plant. These axes were driven by the occurrences of the rare species, such as the protozoan *Colpoda* sp. and some of the bacterial morphotypes (Fig. 1B). The axes were not related to functional groups: the species scores of large invertebrates (dipterans and mites), bacteriovores (protozoa and rotifers), and bacteria did not differ (Axis 1: $F = 0.30$, $P = 0.75$; Axis 2: $F = 0.67$, $P = 0.53$; $df = 2$ in both cases).

Species richness

The only factor to explain a significant amount of the variation in number of species per pitcher was pitcher fluid volume; pitchers containing more fluid were more species rich (Table 1). The model explained just over 62% of the variance in pitcher species richness. Plant total species richness was predicted by plant size (number of pitchers), mean pitcher aperture height, and soil organic matter content beneath the plant (Table 1). More species occurred in plants with more leaves that grew in soil with lower organic-matter content and had pitchers whose apertures were, on average, farther from the ground.

Table 1. Significant results for regression on environmental predictors of total inquiline species richness at the between-pitcher (within plant) and between-plant scales in the pitcher plant *Sarracenia purpurea.* Total plant species richness at both scales was modelled as a function of environmental predictors with generalized linear models with Poisson error distribution. At the between-pitcher scale the categorical variable 'plant' was included as a random effect in a generalized linear mixed model to account for the effects of pitcher pseudoreplication among plants; this random effect was highly significant under a likelihood-ratio test ($P < 0.001$).

Response	Predictor	Model R^2	Slope estimate	Standard error	Type III Likelihood ratio test
Pitcher total species richness	Pitcher fluid volume	0.623	0.027	0.01	20.5***
Plant total species richness	Number of pitchers	0.370	0.089	0.016	29.4***
	Mean pitcher aperture height		0.166	0.039	16.7***
	Soil organic matter content		-0.029	0.010	8.9**

***$P < 0.001$, **$P < 0.01$.

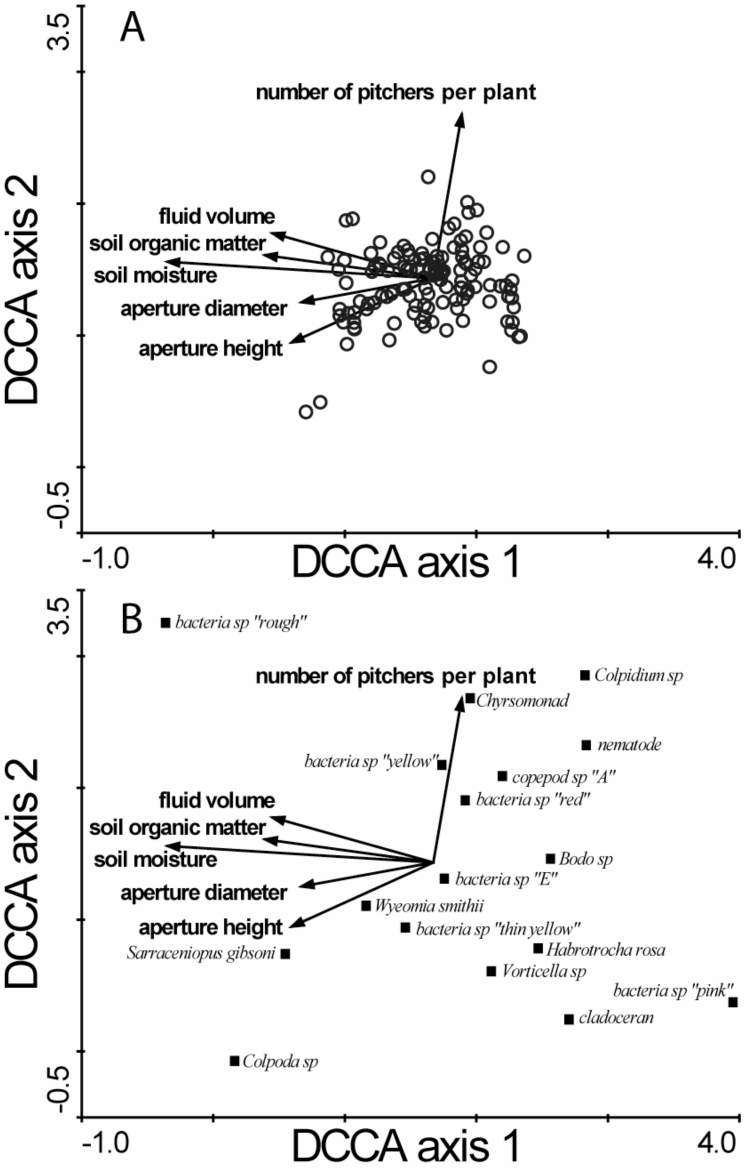

Figure 1. Scatter-plot showing de-trended canonical correspondence analysis (DCCA) axis 1 and axis 2 (A) site scores and (B) species scores and environmental variables. The length of each arrow reflects the importance of that environmental variable.

Table 2. Significant results of logistic regression on environmental predictors of individual species presence in pitchers with 'plant' included as a random effect (where significant as determined by a likelihood ratio test) in a generalized linear mixed model with binomial error assumption. The seven species modelled were those that occurred in at least 20% of pitchers. No significant predictors were found for the three bacterial colony types modelled.

Taxon	Predictor	Likelihood ratio test for 'plant'	Model R^2	Slope estimate	Standard error	Type III likelihood ratio test
Wyeomyia smithii	Protozoan richness	36.8***	0.430	–0.64	0.15	17.4***
	Pitcher fluid volume			0.27	0.06	20.8***
Sarraceniopus gibsoni	Bacterial richness	34.4***	0.516	0.39	0.16	5.6**
	Aperture height			0.68	0.16	17.3***
Habrotrocha rosa	Protozoan richness	0	0.053	0.33	0.11	8.6**
Bodo sp.	Invertebrate richness	20.7***	0.262	0.54	0.18	8.7**
	Aperture height			–0.45	0.13	11.4**
	Pitcher fluid volume			0.11	0.04	7.9**

***$P < 0.001$, **$P < 0.01$.

Predicting the occurrence of individual species

After the clustering of pitchers within plants was accounted for, the occurrences of four of the seven taxa that occurred in more than 20% of pitchers were significantly predicted by measured variables (Table 2). Larvae of *W. smithii*, the pitcher-plant mosquito, were more likely to occur in pitchers containing fewer protozoan species and more fluid. The mite *S. gibsoni* was more likely to occur in pitchers whose apertures were farther from the ground and that contained greater numbers of bacterial colony types. The occurrence of the rotifer *H. rosa* in pitchers was not affected by the plant on which the pitcher occurred (i.e. 'plant' effect) but was affected by protozoan species richness; rotifers were more likely to occur in pitchers that contained more protozoan species. The protozoan *Bodo* sp. was more likely to occur in pitchers containing more invertebrate species, those containing more fluid, and those whose apertures were higher from the ground. None of the three bacterial colony types that occurred in more than 20% of pitchers was significantly related to any of the measured predictors.

Discussion

Previous research has demonstrated that processes occur at least at two spatial scales in inquiline communities associated with *Sarracenia purpurea*: predation and competition occur within pitchers (see, e.g., Kneitel and Miller 2002, Miller et al. 2002a), and dispersal occurs among pitchers (Kneitel and Miller 2003). Because these forces are also expected to operate differently on different species, we expected to observe scale- and species-specific patterns in the 141 inquiline communities from one region. We did find that the communities were highly variable; even pitchers on the same plant shared few species, and environmental and spatial data explained a small but significant amount (22%) of the total variation among pitchers. Spatial and habitat characters contributed roughly equally, so spatial or environmental effects on community structure are either weak, absent, or highly complex. Although relatively few studies are available for comparison, some have found similarly high amounts of unexplained variation in community structure (e.g., Shen and Zhang 2000), whereas others have found evidence of strong gradients related to community patterns (e.g., Skowno and Bond 2003).

The first DCCA axis is related to a gradient in soil moisture and pitcher traits (Fig. 1). Higher soil moisture may produce plants with larger leaves. Larger leaves have greater rates of prey capture (Cresswell 1993) and mosquito oviposition (Heard 1994b), both of which could have direct and indirect effects on inquiline communities. Increased prey capture increases bacterial abundance and can change protozoan abundance and composition (Kneitel and Miller 2002, Miller et al. 2002a), and increased mosquito density is correlated with changes in rotifer and protozoan abundances, as well as protozoan diversity and indirect effects on bacterial abundances and composition (Cochran-Stafira and von Ende 1998, Kneitel and Miller 2002, Miller et al. 2002a). The second DCCA axis was attributed to differences in number of leaves per plant. No mechanism has been demonstrated by which number of leaves per plant might affect the inquiline community, but it could be important if dispersal of some organisms occurred primarily among local pitchers.

Given the significant environmental effects revealed by the DCCA and the known mechanisms that may underlie such patterns, the lack of differences between functional groups in species scores from the DCCA is surprising and suggests that significant unquantified factors obscured these relationships. One possibility is that community (successional) age or age of the leaf strongly affects community patterns (Fish and Hall 1978). New leaves tend to have many more ant prey and mosquitoes (Miller and Kneitel in press); strong resource and predator effects related to leaf age may overwhelm any spatial patterns. We were unable to determine leaf age, but we did note that leaves on the same plant appeared to be produced at regular intervals during the growth season, a pattern that might result in a high variance in community age and composition among leaves on the same plant.

Species richness at both the pitcher and plant scales was best predicted by plant traits. Larger leaves have a greater volume, which was strongly correlated with higher species richness. Similarly, plants with more and taller pitchers had higher species richness. These correlations might arise for either of two reasons: the well-known species-area relationship, which has been attributed both to greater habitat diversity and to the greater stability of larger areas, and the demonstrated tendency of taller pitchers to attract both more prey (Cresswell 1993) and more colonists (Heard 1994b).

The occurrences of some common taxa in the Crystal Savanna community could be predicted by a combination of abiotic and biotic factors. A fairly large proportion of the variance in mosquito-larva abundance and mite (*S. gibsoni*) abundance was predicted by aspects of pitcher size and prey richness (43% and 52%, respectively; Table 2). Abundances of many species appear to be negatively associated with aspects of pitcher size; this is possibly due to the positive correlation of aperture diameter and height with the abundance of the predator mosquito larvae, which in turn may reduce abundances of other species. As noted above, the effect of pitcher size on the abundance of some inquiline species has previously been documented (Heard 1994b). Similarly, mosquito abundances have previously been shown to affect protozoan richness (Kneitel and Miller 2002, Miller et al. 2002a); a similar effect of mites on the richness of their bacterial prey may also be occurring. On the other hand, 26% of the protozoan species *Bodo* sp. and only 5% of rotifer (*H. rosa*) abundances were explained by environmental variables and are difficult to interpret.

The work reported here is unique in several ways. First, we can find no previous study on scale and community patterns that has quantified entire communities. Unfortunately, most studies use the term ‘community’ to refer only to species within a trophic or taxonomic level (recent examples include Skowno and Bond 2003, Jaureguizar et al. 2004). Although community boundaries can be difficult to define, we are confident that we included most of the species in these inquiline communities, incorporating a known food-web structure. Incorporating this more complete suite of interacting species should provide greater insight into factors that control community patterns. Second, most previous studies have inherent difficulties in separating the scales at which processes occur from those at which patterns are sampled or analyzed (Dungan et al. 2002). Because of their discrete nature and the existence of prior experimental work, pitcher plants are a good model system for applying spatial statistical analyses.

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